

The Avian Response to a Population Outbreak of the Tent Caterpillar, *Malacosoma constrictum* (Stretch)

(Lepidoptera : Lasiocampidae)

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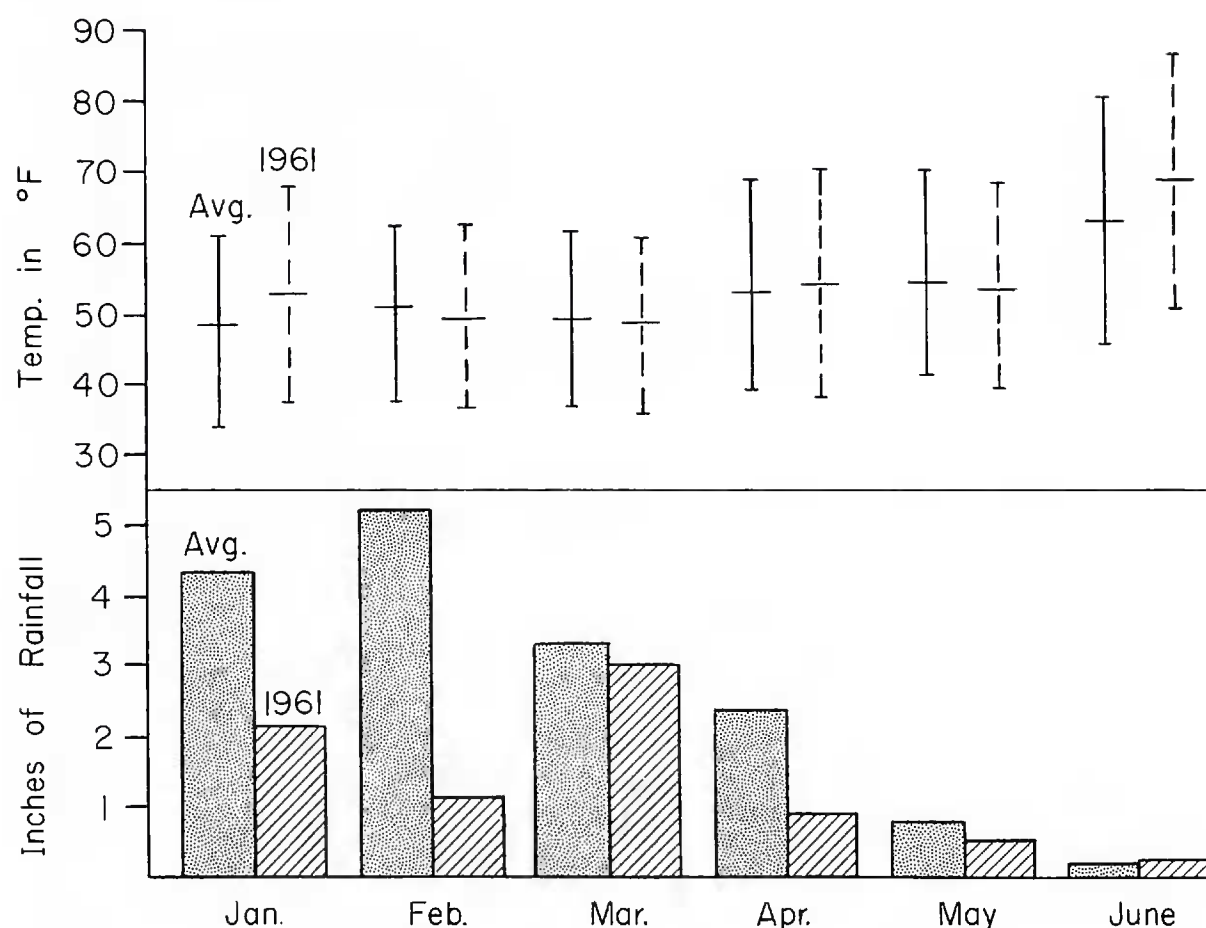
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It is a widely accepted view among biologists that caterpillars which possess numerous, long, integumental hairs are distasteful to most species of insectivorous birds. This view, however, is poorly documented in the literature. During the late spring and summer seasons of 1959–1961, and throughout 1963, I was engaged in a study of the comparative foraging behavior of the insectivorous birds at the Hastings Reservation, Monterey County, California. In the course of this investigation, the abundance of the tent caterpillar, *Malacosoma constrictum* (Stretch), fluctuated widely, thereby making it possible for me to observe how the birds responded to different densities of the “hairy” larvae of this species.

The Hastings Reservation is located in the central Coast Ranges of California where one of the principal vegetation types is a deciduous woodland dominated by blue oaks (*Quercus Douglasii* H. & A.), valley oaks (*Q. lobata* Nee), and hybrid oaks. Coast live oaks (*Q. agrifolia* Nee) are common in the draws and on the shaded lower slopes. The south-facing slopes are covered by a dense chaparral.

During late May and early June 1961, a population outbreak of *M. constrictum* resulted in the almost complete defoliation of the oaks in the vicinity of the Hastings Reservation. Although the temperatures which prevailed during the spring of 1961 were within the normal range, the amount of rain which fell was well below the average for this locality (Fig. 1). By 11 June the defoliation appeared to have reached its fullest extent and the barren oaks were beginning to produce new leaves. At this time caterpillars were very rare, but the ground beneath the defoliated trees was carpeted with pupae and multitudes of adults were attracted to lights at night. In one 48-acre stand of woodland, less than 15% of the individual deciduous oaks escaped complete defoliation. In this area, all of the deciduous oaks exhibited some damage, but scattered clumps of two or three adjacent trees had lost less than 20% of their foliage. Most of the live oaks were attacked, but the larger trees obviously retained more leaves than adjacent deciduous oaks of a comparable size. A few of the scattered madrones

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EXPLANATION OF FIGURE

Fig. 1. A comparison of average spring rainfall and temperatures during a 6-year period (1958-1960, 1962-1964) with conditions in 1961. The temperature data are plotted with the mean of daily highs at the top, the average of daily mean temperatures in the middle, and the mean of daily lows at the bottom.

(*Arbutus Menziesii* Pursh.) were partially defoliated. Signs of obvious defoliation by *M. constrictum* were observed over an area which included at least 1,200 acres of deciduous oak woodland. Within this area, however, scattered enclaves of oaks, varying from a few trees to almost 30 acres in extent, escaped serious damage.

During the spring of 1963, *M. constrictum* again became conspicuous at the Hastings Reservation. This population never reached outbreak proportions: obvious feeding damage was restricted to the foliage associated with one or two branches on scattered deciduous and live oaks. Between 11 March and 29 September 1963 the foliage arthropods were sampled by sweeping the oaks with a heavy insect net at approximately biweekly intervals. A full description of these collections has been reported elsewhere (Root, 1964). The first-instar larvae of *M. constrictum* were first recorded on 28 March during the period when most of the new leaf buds of the deciduous and live oaks were just beginning to

open. The bulk of the population had reached the penultimate and ultimate instars by 8 June although a few caterpillars were observed as late as 27 June. During the period of their occurrence in 1963, the number of tent caterpillars taken in 40 sweeps averaged 8 (range: 1–16) on the deciduous oaks and 11.5 (range: 2–16) on the live oaks. In these collections, the mean abundance of lasiocampid larvae exceeded the numbers of larvae belonging to other lepidopterous families.

Keen (1952), in considering all *Malacosoma* spp., has written: "Birds also play an active part in controlling the tent caterpillars; many species feeding on the caterpillars, others feeding on the eggs, and still others on the moths." At the Hastings Reservation there is good reason to believe that the larvae of *M. constrictum* are distasteful to the majority of the insectivorous birds. During 1963, when the caterpillars formed a conspicuous proportion of the foliage arthropod fauna, adult blue-gray gnatcatchers (*Polioptila caerulea*) were never seen to bring tent caterpillars to their nestlings in the course of 50 hours of close observation at ten different nests. The stomachs of four nestling gnatcatchers collected on 1 June 1963, from a territory where tent caterpillars were especially abundant, contained three noctuid and four geometrid larvae ranging from 15.1 to 19.5 mm in total length. Lepidopterous larvae made up 43.9% of the arthropods found in the nestlings' stomachs. At this time, nearly one-third of the tent caterpillars on this territory were less than 20.0 mm in length and yet they were absent from the birds' diet. On one occasion, when a tent caterpillar of intermediate size crawled onto the nest rim, the adult gnatcatcher seized the larva with its beak and carried it about 20 feet away. This larva was not eaten; after seeming to squeeze it once, the gnatcatcher immediately dropped the caterpillar and vigorously wiped its beak against the perch for a few seconds.

On numerous occasions during 1961 and 1963 I observed foraging warbling vireos (*Vireo gilvus*)², Hutton vireos (*Vireo huttoni*), orange-crowned warblers (*Vermivora celata*), plain titmice (*Parus inornatus*), and gnatcatchers to pass within 2 feet of tent caterpillars without attempting to feed upon them. The stomach contents from these bird species (Table 1) show that larvae of comparable size in other, less conspicuous, lepidopterous families were frequently captured.

The cuckoos, *Coccyzus americanus* and *C. erythrophthalmus*, eat large numbers of "hairy" caterpillars, including *Malacosoma* spp. (Beal

² It is of interest that the stomach of one warbling vireo, collected near Berkeley, California, on 29 April 1962 contained the remains of the larvae of 14 California oak moths, *Phryganidia californica* Packard (Lepidoptera: Dioptidae). These larvae were all about 12 mm in length. Harville (1955) states that *P. californica* seems to be an undesirable food of most birds.

TABLE 1. Numbers of lepidopterous larvae in the diets of insectivorous birds at the Hastings Reservation during the period of 1 May–31 July 1959, 1961, and 1963. Certain characteristics of the sample are also presented.

	<i>Vireo gilvus</i>	<i>Vireo huttoni</i>	<i>Vermivora celata</i>	<i>Polioptila caerulea</i>	<i>Parus inornatus</i>
Tortricidae	13				
Pyralidae			4	2	
Geometridae	52	14	9	5	
Noctuidae	17	16	3	13	4
Arctiidae	1		1	1	
No. of stomachs examined	17	18	5	29	19
Per cent of stomachs containing caterpillars	100	72	100	52	39
Length of caterpillars in mm, $\bar{X}$ (range)	14.8 (7–30)	16.1 (9–26)	15.1 (7–26)	14.3 (8–25)	20.0 (12–26)

and Judd, 1898; Bent, 1940). Indeed, these birds seem to be attracted to areas of eastern tent caterpillar (*M. americanum* (Fabricius)) outbreaks during the breeding season. The thin, smooth-walled stomachs of these birds are frequently felted by the penetration of hairs from the caterpillars; Forbush (1927) states that cuckoos are able to shed their stomach linings when they become completely matted with these hairs. *Coccyzus erythrophthalmus* does not occur within the range of *M. constrictum*, however, and *C. americanus* is restricted to the valley-floor riparian woodlands in California (Miller, 1951) where it has infrequent contact with this caterpillar.

On two occasions, Bullock orioles (*Icterus bullockii*) were observed to eat late-instar larvae of *M. constrictum* at the Hastings Reservation (C. G. Sibley, field notes). In each case, the oriole grasped the larva in its beak at one end of the body and beat the caterpillar against the perch until the integument was shucked off. The skin was left behind while the remainder of the caterpillar was eaten. Following ingestion, the orioles wiped their beaks against a branch. During 1961, there was no indication of an increase in the density of Bullock orioles, suggesting that this species is not particularly attracted to areas of tent caterpillar outbreaks.

The nesting activities of most of the insectivorous birds in the oak woodlands at the Hastings Reservation seemed to collapse during the 1961 defoliation by tent caterpillars. Between 11 and 15 June I ob-

TABLE 2. The diets of blue-gray gnatcatchers collected in the oak woodlands at the Hastings Reservation during June of different years. The data are presented as the per cent of the total individuals (N) in each sample.

	1960	1961 ¹	1963
Hemiptera	50.8	44.3	41.2
Lepidoptera	2.5	11.4	13.7
Diptera	7.5	5.7	3.9
Coleoptera	14.6	20.0	29.5
Hymenoptera	15.6	15.7	7.8
Araneae	9.0	2.9	3.9
N	122	70	51

¹ All specimens were collected in areas of extensive defoliation by *M. constrictum*.

served several pairs of gnatcatchers, vireos, and warblers which were without nestlings or fledglings. Normally, early June constitutes the peak of the breeding season for these birds (Root, 1964). One pair of titmice was accompanied by fledglings. This species is a permanent resident of the deciduous woodland, and is well adapted for foraging in the barren limbs and branches of the oaks. At this time, all of the gnatcatchers observed on the area were starting to build new nests in oaks which had escaped serious defoliation.

The diet of gnatcatchers in large stands of defoliated oak woodland during early June 1961 did not differ greatly from the June diet in years when tent caterpillars were at lower densities (Table 2). The widespread defoliation probably reduced the populations of the foliage arthropods which constitute a major proportion of these birds' diet. Such a failure in the food supply could result in a cessation of avian breeding activity.

Despite their extreme abundance during June 1961, the adults of *M. constrictum* were not found in the stomachs of the gnatcatchers collected at that time. These same stomachs, however, contained the adults of two pyralids, one geometrid, and one noctuid.

These observations suggest that birds are not likely to be effective in controlling populations of *M. constrictum*. Langston (1957) states that the integumental hairs of tent caterpillars discourage attack by arthropod parasites and predators. Judging from the behavior exhibited by birds while handling these insects, it would appear that the hairs serve an additional function as a protective device against avian predators.

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CORRECTION

The statement by Butler and Ritchie in *Pan-Pacific Entomologist* 41 (3): 156, "It (*Anthrax cinctalpa* Cole) was reared by R. W. Thorp from both *M. rotundata* and *M. concinna* in California" is in error. It was reared only from *M. concinna*.—G. D. BUTLER, *University of Arizona, Tucson*, and R. W. THORP, *University of California, Davis*.